

## Effects of post-larval abalone (*Haliotis rubra*) grazing on the epiphytic diatom assemblage of coralline red algae

Sabine Daume<sup>1</sup>, Sascha Brand, and Wm. J. Woelkerling

School of Botany, La Trobe University  
Bundoora, Victoria 3083

<sup>1</sup> Corresponding author.

E-mail: botsd@lure.latrobe.edu.au

### Abstract

Larvae of the abalone *Haliotis rubra* were settled on pieces of the non-geniculate coralline red alga *Phymatolithon repandum*. We measured a mean growth-rate of ca. 30  $\mu\text{m}/\text{day}$ , 11 days after larval settlement which stayed constant throughout the experiment. The diatom assemblage on the surface of the alga was studied for 53 days after larval settlement using scanning electron microscopy. Two species of the genus *Cocconeis* were found to dominate the diatom assemblage on the surface of *P. repandum*. Up to 18 days after larval settlement, the diatom population increased exponentially. Eighteen days after settlement, post-larval abalone started to graze on the diatom *Cocconeis scutellum* leaving the bottom valves of the diatoms on the surface of *P. repandum*. As a result, the diatom population decreased markedly. The outermost cells and polysaccharide layer of *P. repandum* were often missing but we did not find any grazing marks on the thallus surface up to 53 days post-settlement. We discuss the hypothesis that epithallial cell sloughing of non-geniculate coralline red algae is an intrinsic mechanism to reduce microscopic epiphytes and may interact closely with grazing by post-larval abalone. We concluded that the post-larvae must find an additional food source derived from the NCA before grazing on the diatoms, because of the high growth-rate during the first and second week of rearing and the constancy throughout the experiment.

### Introduction

The relationship between abalone and non-geniculate coralline red algae (NCA) (Corallinales, Rhodophyta) is well known. Abalone larvae settle on NCA (Morse & Morse 1984; 1988; Morse 1990; 1991) and remain in the coralline habitat until they are about 6 mm in shell length (Shepherd & Daume 1996). Post-larval abalone are known to feed on benthic diatoms (Kawamura *et al.* 1995). Diatoms occurring on artificial plates have also been used as the initial food source in commercial abalone hatcheries. Recent interest has focused on settlement and feeding experiments of post-larval abalone on species of benthic diatoms (Kawamura & Kikuchi 1992; Kawamura & Takami 1995; Kawamura *et al.* 1995; Matthews & Cook 1995; Kawamura 1996). Despite the importance of diatoms in abalone feeding ecology, the naturally occurring diatom assemblage on the NCA surface has never been studied in detail.

Molluscan herbivores have a major effect on the algal community by feeding on the sporelings of macroalgae (Dayton 1975; Menge 1976; Underwood & Jernakoff 1981). If herbivores are removed, the macroflora increases. This effect has been well documented in the past (Southward 1964; Dayton 1971) and later tested at the microflora level (Nicotri 1977; Underwood 1984) however, the influence of post-larval abalone grazing on the diatom assemblage of NCA surfaces has not been investigated.

*Phymatolithon repandum* (Foslie) Wilks and Woelkerling 1994 and other species of NCA frequently slough epithallial cells, and this has been interpreted as an antifouling mechanism which



inhibits algal spore settlement (Masaki *et al.* 1984; Johnson & Mann 1986; Keats *et al.* 1993; 1997). The effects of epithelial cell sloughing on the diatom assemblage of NCA surfaces is described in this study.

Herbivores like *Cellana* spp., *Acmaea* spp., *Notoacmaea* spp., *Patella* spp. as well as *Haliotis* spp. are known to leave grazing marks produced by the specialized teeth of their radula while feeding on NCA (Clarkson & Shepherd 1985; Padilla 1985; Garland *et al.* 1985). Garland *et al.* (1985) described grazing marks of 6 week old post-larvae which were 1–2 cells deep. It is unknown however, if post-larval abalone younger than 6 weeks leave grazing marks on the thallus surface.

In this paper we describe:

- (1) the distribution of the dominant diatom species on the surface of the NCA *Phymatolithon repandum*;
- (2) the effect of post-larval abalone grazing on the dominant diatom species from day of larval settlement to 53 days after settlement;
- (3) cell sloughing on different growth-forms of *P. repandum* and the effect it has on the diatom assemblage; and
- (4) the radula structure and teeth arrangement of post-larval abalone.

## Materials and Methods

### Sampling

Small rocks encrusted with NCA were collected from a boulder habitat in front of the Gloucester Reserve, Williamstown, Victoria, Australia (37° 53'S, 144° 55'E) at 3–4 m depth. Williamstown is located at the north end of Port Phillip Bay and is close to Port Melbourne and the mouth of the Yarra River. Only the blacklip abalone, *Haliotis rubra* Leach 1814 is present here. *Phymatolithon repandum* is the dominant NCA species at this locality (unpublished data) and occurs with two different growth-forms (encrusting and warty, see Woelkerling *et al.* 1993). Pieces (ca. 1 cm<sup>2</sup>) of each growth-form were removed from the rocks with a razor blade or chisel. Each replicate for the diatom study and the experiment was obtained from a different plant to ensure independence.

### Distribution of the dominant diatoms on *P. repandum*

Pieces of the encrusting and warty growth forms were freshly collected and air dried after sampling to study the composition and distribution of diatoms on the thallus surface. The samples were mounted on aluminium stubs with 'Fotobond' acrylic adhesive (Agfa-Gevaert Ltd). The stubs were sputter-coated with gold before viewing in a Siemens ETEC Autoscan microscope at 20 kV to determine the frequency of diatom occurrence on the two growth-forms of *P. repandum*. For each sample, the presence or absence of diatom species was recorded at a magnification of 1200x in 20 fields of view.

### Effect of post-larval grazing

Larvae of the abalone *Haliotis rubra* obtained from a hatchery (Cheetham Salt, Lara, Victoria, Australia) were allowed to settle onto surfaces of *Phymatolithon repandum*. Two pieces of *P. repandum* (ca. 1 cm<sup>2</sup>) representing the encrusting and warty growth forms were placed in each of 24 sterile glass jars with 300 ml UV sterilised sea water. Jars were kept at 15° C, 3000 lux with a 12 h L:D photo cycle. One hundred larvae competent to settle were added to each of 18 jars. Six jars, without larvae and only the warty growth-form, were used as a control. The shell length of four randomly chosen larvae was measured before being added to the jars. Three to four larvae were measured 11, 18 and 53 days after settlement to calculate their growth-rate.

Less than 20 larvae/cm<sup>2</sup> were maintained on each piece of NCA. Abalone were observed moving over the NCA surface through a dissecting microscope, showing side to side scraping by the radula and judged to be actively feeding.



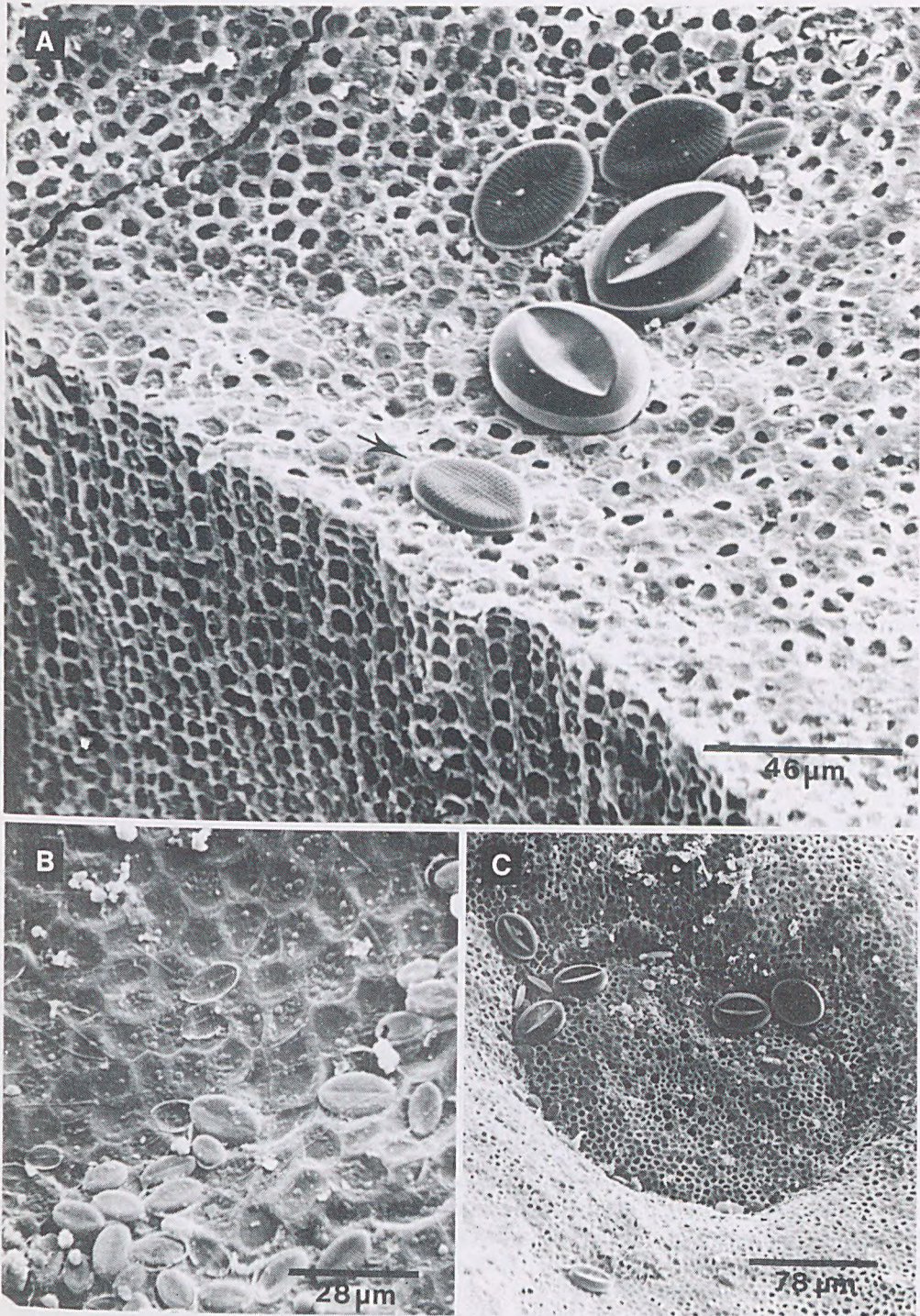


Figure 1. Diatoms (*Cocconeis* spp.) on the surface of *Phymatolithon repandum*. A: Two species of *Cocconeis*: *Cocconeis scutellum* (arrow) and *Cocconeis* sp. B: Diatoms occur in a patchy distribution. C: Diatoms proliferate around conceptacles.



### Diatom distribution under grazing pressure and cell sloughing of NCA

Pieces of both NCA growth-forms with post-larvae and pieces from the control jars (without post-larvae) were subsampled randomly 4, 11, 18, 30 and 53 days after larval settlement. The subsamples were air dried and treated for the scanning electron microscopy (SEM) study as described above. For each sample, the presence or absence of diatom species and cell sloughing was recorded at a magnification of 1200x and 150x respectively in 20 fields of view. The mean frequency ( $\pm$  standard error) of diatom species and cell sloughing was calculated.

### Abalone radula

To study the post-larval abalone radula, the shell was removed, the tissue of the whole animal dissolved in 6% sodium hypochlorite overnight, washed in distilled water, allowed to dry and then prepared for SEM as described above.

### Data analysis

Statistical analyses were carried out using the STATISTICA (Statsoft Inc. 1995) computer package. One-way and two-way ANOVAs were carried out on untransformed data (number of fields with *Cocconeis* spp.) followed by Tukey's multiple comparison test.

## Results

### Distribution of the dominant diatoms on *P. repandum*

During the period of the study (October to December 1995) only pennate diatoms were observed on the surface of *P. repandum*. The genus *Cocconeis* was represented by two species (*Cocconeis scutellum* (Ehrenberg) Boyer 1927; *Cocconeis* sp.) (Fig. 1A) that dominated the diatom assemblage. On all samples examined, they formed 90–100% of the diatom population with a size range from 10 to 40  $\mu\text{m}$ . We observed a low frequency (5–10%) of diatoms on freshly sampled pieces of both growth-forms of *P. repandum*. All diatoms were found in a patchy distribution (Fig. 1B) and proliferated in cavities and around conceptacles (Fig. 1C).

### Effect of post-larval grazing

The frequency of *Cocconeis* spp. on the surface of *P. repandum* grazed by post-larval abalone changed during the period of study (Fig. 2). Between four and 11 days after abalone larvae settled on the NCA surface, the frequency of *Cocconeis* spp. increased exponentially on both growth-forms of NCA but not on the controls where larvae were absent. *Cocconeis* spp. reached a maximum frequency of 80% on the encrusting growth-form 11 days after larval settlement (Fig. 3A). There was a highly significant difference in frequency of *Cocconeis* spp. between the control and the 2 treatments with post-larval abalone 11 and 18 days after settlement (2-way ANOVA, Treatment  $\times$  Age Interaction,  $p < 0.001$ ). However, there was no significant difference in diatom frequency between the warty and the encrusting growth-form throughout the experiment (2-way ANOVA,  $p = 0.24$ ).

After 18 days, the *Cocconeis* population decreased on both treatments with post-larval abalone (Fig. 2). On the grazed surfaces, raphe-bearing valves (bottom valves) of *C. scutellum*, ca. 20  $\mu\text{m}$  in length, appeared approximately 18 days after larval settlement (Fig. 3B), suggesting that post-larval abalone were removing the top valves of the diatom and thus gaining access to the diatom cell contents.

The growth-rate of the post-larval abalone was relatively constant throughout the experiment with a mean growth-rate of 31.4  $\mu\text{m/day}$  (S.E. 5.2  $\mu\text{m}$ ) 11 days after settlement, 33.3  $\mu\text{m/day}$  (S.E. 1.4  $\mu\text{m}$ ) 18 days after settlement and 33.9  $\mu\text{m/day}$  (S.E. 0.8  $\mu\text{m}$ ) 53 days after settlement.

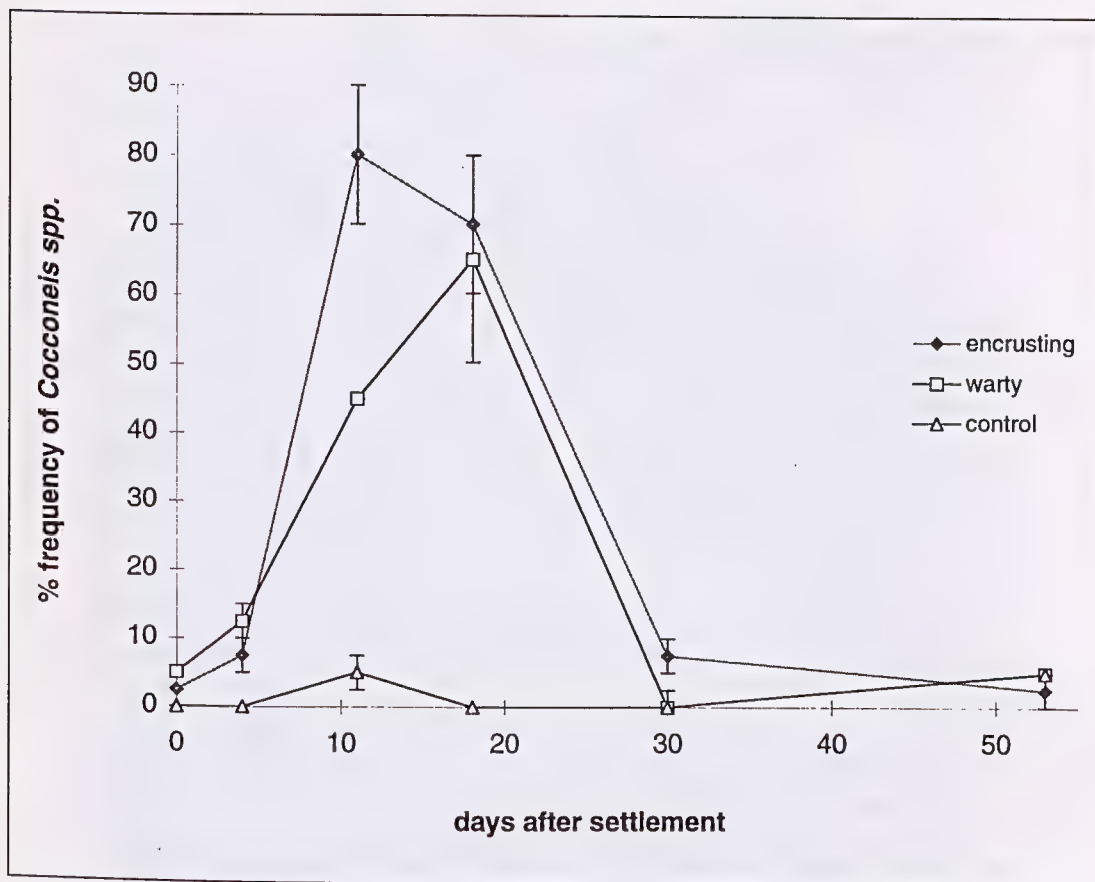


Figure 2. Changes in frequency of occurrence of *Cocconeis* spp. on the surface of *Phymatolithon repandum* when grazed by post-larval abalone (*Haliotis rubra*). Vertical bars indicate the standard error.

### Cell sloughing of NCA

Cell sloughing was observed on the control pieces of *P. repandum* and occurred significantly more on the warty than on the encrusting growth-form of the treatment (1-way ANOVA,  $p < 0.047$ ). The mean frequency of cell sloughing was 16% (S.E. 4.3%) for the encrusting and 45% (S.E. 12.1%) for the warty growth-form. Cell sloughing was intense both around and between warty protuberances (Fig. 4A). Figure 4B shows an area of intensive sloughing in detail. The outermost cells become detached in sheets of numerous cells and subsequently removes all epiphytes occurring on the surface.

### Abalone radula

The post-larval abalone radula has numerous teeth per row (Fig. 5A). Each row consists of 1 median tooth with a smooth edge, 5 (2+3) strong lateral teeth on each side with sharp endings for rasping, and numerous marginal teeth with serrated edges. The marginal teeth are similar to the outermost lateral teeth, but become progressively thinner.

Each tooth has a width-to-length ratio of approximately 1:2. The teeth of *Haliotis rubra* have a clearance angle (angle from the coralline surface to the back of the tooth) of about  $8^\circ$ .





Figure 3. Abalone post-larvae grazing on the surface of *Phaeosaccellon repandum*. A: Post-larvae 11 days after settlement. *Cocconeis* sp. proliferating on the surface. B: Grazed surface of NCA with bottom, raphe-bearing valve of the diatom *Cocconeis scutellum* still attached to the surface.

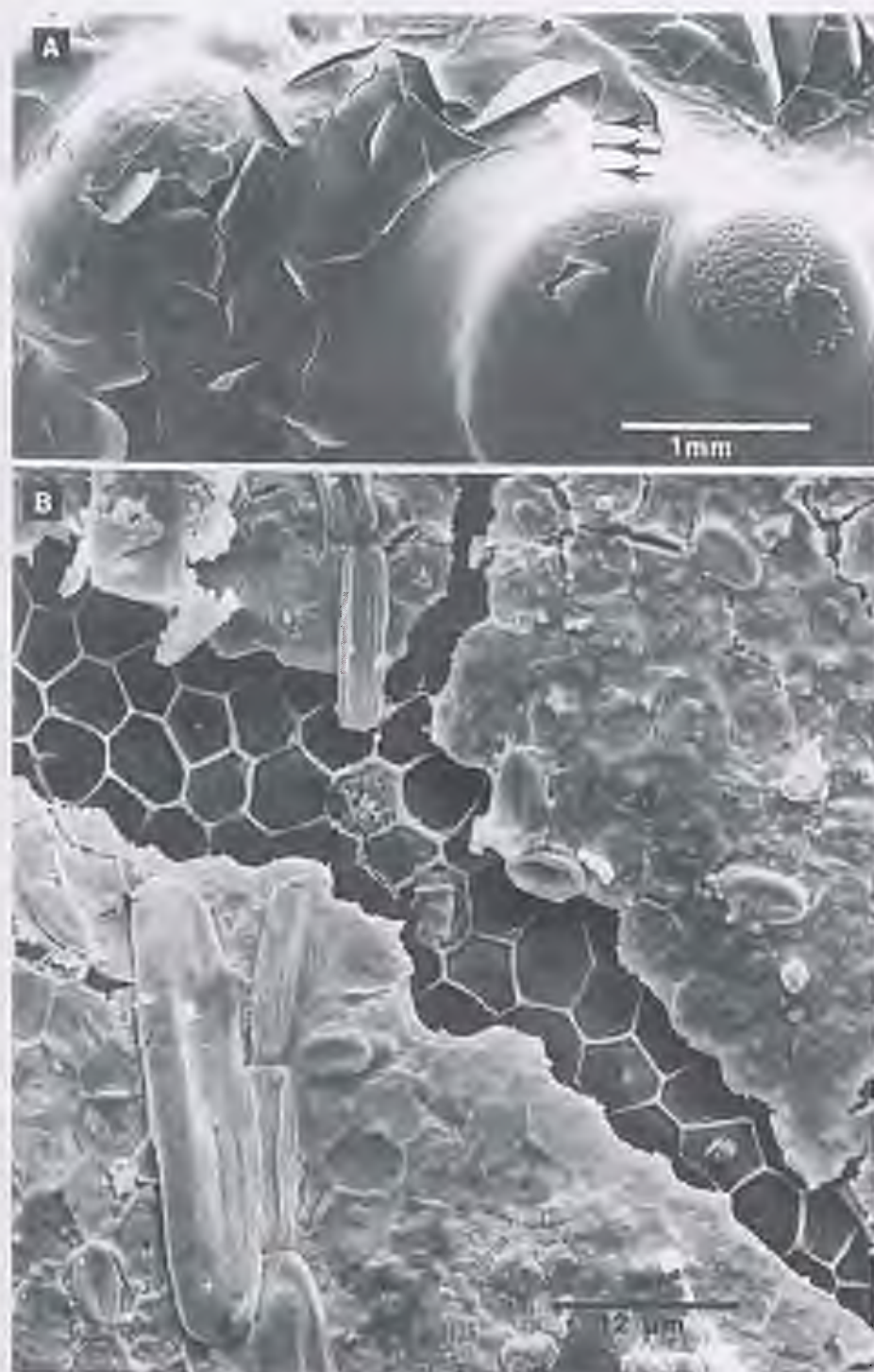


Figure 4. Epithelial cell sloughing of *Phymacthion repandum*. A. Warty growth-form with intensive cell sloughing (arrows). B. Outermost layer of cells sloughing off and effectively remove diatoms growing on the surface.



Grazing marks matching the pattern of post-larval abalone radulae were not found on the surface of *P. repandum* during the 53 days after settlement. The polysaccharide layer together with the outermost cells of the thallus were often missing on both the grazed and ungrazed (control) pieces.

## Discussion

### Distribution of the dominant diatoms on *P. repandum*

The low frequency of diatoms observed on freshly sampled NCA is comparable to non-living substrata such as rocks but not other macroalgae (Round *et al.* 1990). Non-living substrata are less favourable to diatom growth than macroalgae and seagrasses and thus support a low frequency of diatoms (Hudson & Bourget 1981).

Eckman and Norwell (1984) noticed that on the bottom of bumps, areas with a specific horseshoe vortex effect of flow, the microbial activity and mucus binding capacity is enhanced. Consequently, we expected a higher frequency of diatom occurrence on the warty growth-form. However, we did not notice any difference between the two growth-forms, neither on freshly sampled pieces or on pieces sampled throughout the experiment. The observed higher frequency of cell sloughing on the warty growth-form (warty treatment and control) could have offset the expected growth-form effect and thus the frequency of diatoms was similar on both growth-forms of *Phymatolithon repandum*.

In this study, species of *Cocconeis* were observed to be the dominant diatoms on the surface of *P. repandum*. In agreement with our findings, Kawamura *et al.* (1992) observed that in areas dominated by crustose coralline algae, diatoms with strong adhesive solitary forms such as *Cocconeis* spp. dominate the benthic diatom population. In addition, Hudon and Bourget (1981) found that *Cocconeis* spp. and *Amphora* spp. were the first and major colonizers on artificial plates from May to mid August (northern hemisphere). They noticed a change in diatom dominance at the beginning of September which suggests that the dominance of *Cocconeis* spp. may be seasonal.

### Effect of post-larval grazing

Four to 11 days after larval settlement the populations of *Cocconeis* spp. increased exponentially on both growth-forms of NCA. We did not find any bottom valves of diatoms on the NCA surface at this young age, suggesting that post-larval abalone do not graze on *Cocconeis* spp. at this stage. Species of *Cocconeis* are known to have high adhesive strength (Kawamura *et al.* 1995) and young post-larvae might not be able to detach the valves from the surface of *P. repandum*. In addition, competing diatoms and bacteria may have been preferentially consumed at this early stage. Young post-larvae are known to feed on loosely attached diatoms. The extracellular mucus associated with these diatoms is considered to be a good food source (Kawamura and Takami 1995; Kawamura 1996). The grazing activity and metabolic processes of post-larvae up to 11 days after larval settlement, seems to allow the *Cocconeis* population to proliferate which ensures enough food supply for the abalone in coming weeks. In the control, without abalone grazing activity, the *Cocconeis* population never exceeded a 5% frequency. In agreement, Suzuki *et al.* (1987) and Matthews and Cook (1995) noted that under the grazing pressure of juvenile abalone, prostrate diatoms like *Cocconeis* spp., start to proliferate. After several days artificial plates are covered entirely with these diatoms (Suzuki *et al.* 1987). However, none of them observed post-larvae or juveniles grazing on *Cocconeis* spp.

We measured a mean growth-rate of ca. 30  $\mu\text{m}/\text{day}$  11 days after settlement which stayed relatively constant throughout the experiment. Garland *et al.* (1985) settled larvae of *Haliotis rubra* onto NCA in 1000-l culture bins. The larvae grew to a mean size of  $692 \pm 33 \mu\text{m}$  in 42 days (10.5  $\mu\text{m}/\text{day}$ ) which is considerably lower than the growth-rate we calculated. However, they did not have any measurements for the first two weeks of rearing. Kawamura and Takami (1995) measured the mean growth-rate of the post-larval abalone *Haliotis discus hannai*, settled in tissue culture wells with only *Cocconeis scutellum* as a food source. They recorded a growth-rate of  $24.7 \pm 1.6 \mu\text{m}/\text{day}$



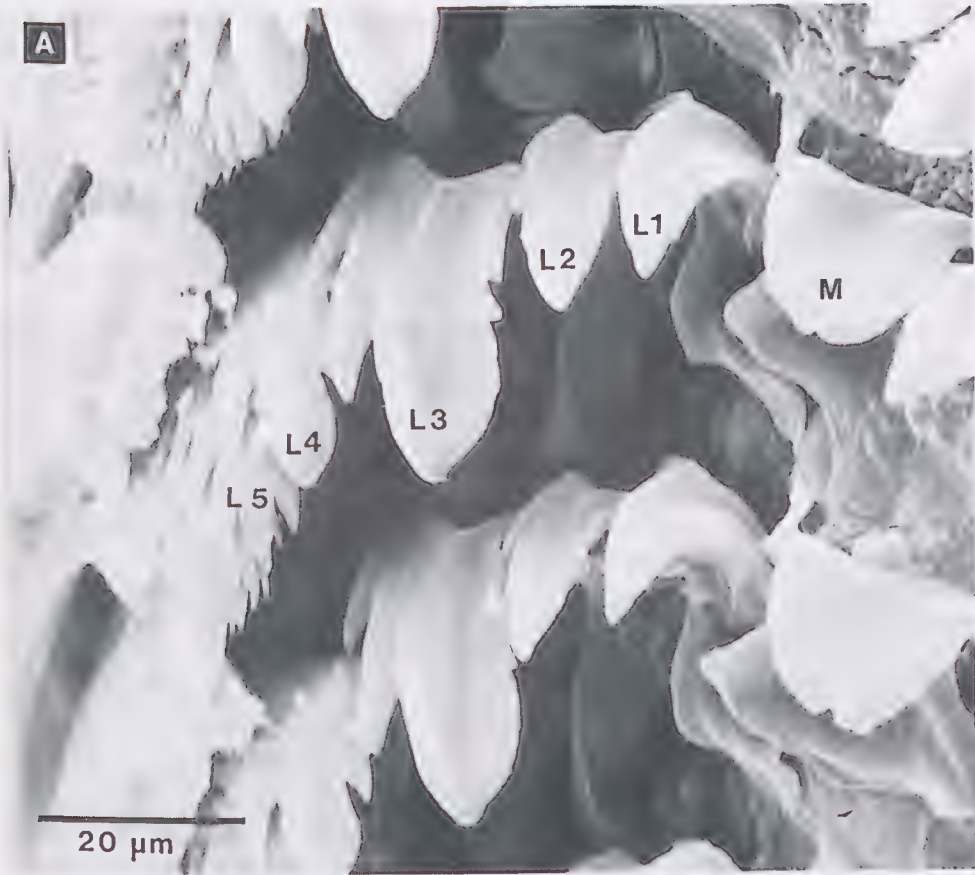


Figure 5. Part of the radula of a post-larval abalone (*Haliotis rubra*) with 1 median (M) and 5 lateral teeth (L1–L5).

from 0 to 10 days after settlement. The growth rate decreased 10 days after settlement ( $7.5 \pm 2.1 \mu\text{m/day}$ ) and was significantly lower than those of abalone fed on other species of diatoms. Takami *et al.* (this issue) settled abalone larvae of the same species onto small rocks encrusted with the NCA (*Lithophyllum yessoense*). When treated with  $\text{GeO}_2$  to reduce the diatom growth on surfaces of *L. yessoense*, the growth-rate of the abalone did not differ from untreated *L. yessoense* surfaces during the first seven days of rearing. However, the growth-rate of the post-larvae *H. discus hannai* in this experiment was both constant and higher on the surface of *L. yessoense* (treated  $37.0 \pm 0.7 \mu\text{m/day}$  and untreated  $40.9 \pm 0.7 \mu\text{m/day}$ ) compared to Kawamura and Takami's (1995) experiment, in which the larvae were grown on diatoms only. In agreement with our results, this suggests that post-larval abalone must find an additional food source derived from the NCA rather than the diatoms occurring on its surface. This food source is important during the first week of rearing.

Giraud and Cabioch (1976) describe a layer of polysaccharide material covering the external part of the thallus of a variety of different species of NCA. The cells just below that layer have uncalcified cell walls at their external pole and vesicles full of polysaccharide fibrils which can open through the plasmalemma and diffuse into the outermost layer. Garland *et al.* (1985) suggested that post-larval abalone (6 weeks old) graze on the surface mucus, polysaccharide layer and the epithelial cell content of the NCA.

Diatoms with valves which can be ruptured by the abalone radula, such as the valves of *Cocconeis* spp., are considered to be a high value food source for post-larval abalone, approximately 1 mm in



shell length (Kawamura 1996). Our findings suggest that post-larvae of *Haliotis rubra* start feeding on diatoms about 18 days after settlement, when they are approximately 800  $\mu\text{m}$  in shell length. In addition, Takami *et al.* (1997b) stated that post-larvae of *H. discus hannai* are able to access diatom cell contents once they reach about 800  $\mu\text{m}$ . Takami *et al.* (this issue) found a higher growth-rate of *Haliotis discus hannai* fed on NCA with diatoms, than on NCA without diatoms, 2 weeks after settlement. In agreement with our findings this also suggests that the NCA alone provides enough food for the post-larvae until 2 weeks after settlement and /or post-larvae can not utilize the diatom food source until approximately 2 weeks after larval settlement.

### Cell sloughing of NCA

Cell sloughing was observed on the control pieces and more frequently on the warty than on the encrusting growth-form of *P. repandum*. This difference could explain the lower frequency of diatoms on the warty growth-form in Fig. 2 and the overall low diatom frequency of the ungrazed control. It also suggests that cell sloughing intrinsically controls overgrowth by diatoms and other epiphytes when grazers are absent. Cell sloughing may also facilitate the occurrence of early successional diatom species such as *C. scutellum* (Hudson and Bourget 1981) by providing new, uncolonised substrata.

The polysaccharide layer together with epithallial cells of the coralline thallus were partially missing on all pieces observed. Garland *et al.* (1985) report that post-larvae (6 and 13 weeks old) of *Haliotis rubra* remove and ingest the polysaccharide layer and epithallial cells of NCA. In this study grazers in the field (before the NCA had been sampled) or the post-larval abalone (up to 53 days after settlement) might have removed the outermost cells and polysaccharide layer without leaving any obvious, deeply penetrating grazing marks.

### Abalone radula

Abalone have a rhipidoglossan radula like many primitive herbivorous prosobranchs (Crofts 1929). The teeth of post-larval abalone have a low clearance angle. A clearance angle close to  $0^\circ$  results in a tooth sliding across the surface rather than cutting into the surface of the algae (Padilla 1985). This might explain why we did not observe grazing marks of post-larval abalone on the surfaces of *P. repandum*. Given the low clearance angle of the teeth, it seems that abalone post-larvae would be more efficient grazers on flat surfaces *eg.* encrusting compared to a warty growth-form of NCA.

We concluded that abalone post-larvae must find an additional food source derived from the NCA before grazing on the diatoms, because of the high growth-rate during the first and second week of rearing and the constancy throughout the experiment.

Both mechanisms, the cell sloughing of *P. repandum* and grazing by post-larvae, seem to enhance the quality of the diatom assemblage on NCA as a food source for post-larval abalone. Cell sloughing controls overgrowth by diatoms and other epiphytes (Keats *et al.* 1997) which is known to be advantageous during the early life history of abalone (Shepherd & Daume 1996). Grazing by post-larval abalone seems to encourage proliferation of *Cocconeis* spp. which provides a good food source for the coming weeks.

Further experiments are required to gain a better understanding of the interactions of both mechanisms on epiphytic diatom assemblages and their effect on abalone settlement and early growth.

### Acknowledgments

We are grateful to Tony Smith and Peter Rankin from Ridley Corporation Ltd., Division of Pet Products and Emerging Businesses, Victoria for the supply of abalone larvae. We thank Dr .T. Kawamura for confirming the diatom identifications, Trevor Phillips for assistance with photography, Dr. Scoresby Shepherd and Adela Harvey for helping to improve the manuscript and



Stephen Madigan and an anonymous reviewer for their useful comments. This study was supported by an ARC collaborative research grant in association with the South Australian Research and Development Institute and a La Trobe University post-graduate scholarship to the first author.

#### Literature cited

- Clarkson, P.S. and Shepherd, S.A. 1985. Distribution and feeding of archaeogastropods in a boulder habitat at West Island, South Australia. *Journal of the Malacological Society of Australia* 7(1-2): 35-44.
- Crofts, D.R. 1929. *Haliotis*. Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals 29: 55-64.
- Dayton, P.K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351-389.
- Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45: 137-159.
- Eckman, J.E. and Nowell, A.R.M. 1984. Boundary skin friction and sediment transport about an animal-tube mimic. *Sedimentology* 31: 851-862.
- Garland, C.D., Cooke, S.L., Grant, J.F. and McMeekin, T.A. 1985. Ingestion of the bacteria on and the cuticle of crustose (non-articulated) coralline algae by post-larval and juvenile abalone (*Haliotis ruber* Leach) from Tasmanian waters. *Journal of Experimental Marine Biology and Ecology* 91: 137-149.
- Giraud, G. and Cabioch, J. 1976. Étude ultrastructurale de l'activité des cellules superficielles du thalle des Corallinacées (Rhodophycées). *Phycologia* 15(3/4): 405-414.
- Hudon, C. and Bourget, E. 1981. Initial colonization of artificial substrate: Community development and structure studied by Scanning Electron Microscopy. *Canadian Journal of Fishery and Aquatic Science* 38: 1371-1384.
- Johnson, C.R. and Mann K.H. 1986. The crustose coralline alga, *Phymatolithon* Foslie, inhibits the overgrowth of seaweeds without relying on herbivores. *Journal of Experimental Marine Biology and Ecology* 96: 127-146.
- Kawamura, T. 1996. The role of benthic diatoms in the early life stages of the Japanese abalone *Haliotis discus hannai*. Pp. 355-367. In: Watanabe, Y., Yamashita, Y. and Oozeki, Y. *Survival Strategies in Early Life Stages of Marine Resources*. Balkema, Rotterdam.
- Kawamura, T. and Kikuchi, H. 1992. Effects of benthic diatoms on settlement and metamorphosis of abalone larvae. *Suisanzoshoku* 40: 403-409.
- Kawamura, T., Yamada, H., Asano, M. and Taniguchi, K. 1992. Benthic diatom colonizations on plastic plates in the sublittoral zone of Oshika Peninsula, Japan. *Bulletin of Tohoku National Fisheries Research Institute* 54: 97-102.
- Kawamura, T. and Takami, H. 1995. Analysis of feeding and growth rate of newly metamorphosed abalone *Haliotis discus hannai* fed on four species of benthic diatom. *Fisheries Science* 61: 357-358.
- Kawamura, T., Saido, T., Takami, H. and Yamashita, Y. 1995. Dietary value of benthic diatoms for the growth of post-larval abalone *Haliotis discus hannai*. *Journal of Experimental Marine Biology and Ecology* 194: 189-199.
- Keats, D.W., Groener, A. and Chamberlain, Y.M. 1993. Cell sloughing in the littoral zone coralline alga *Spongites yendoii* (Foslie) Chamberlain (Corallinales, Rhodophyta). *Phycologia* 32: 143-152.
- Keats, D.W., Knight, M.A. and Pueschel, C.M. 1997. Antifouling effects of epithallial shedding in three crustose coralline algae (Rhodophyta, Corallinales) on a coral reef. *Journal of Experimental Marine Biology and Ecology* 213: 281-293.
- Masaki, T., Fujita, D. and Hagen, N.T. 1984. The surface ultrastructure and epithallium shedding of crustose coralline algae in an 'Isokayake' area of south western Hokkaido, Japan. *Hydrobiologia* 116/117: 218-223.
- Matthews, I. and Cook, P.A. 1995. Diatom diet of abalone post-larvae (*Haliotis midae*) and the effect of pre-grazing the diatom overstorey. *Marine and Freshwater Research* 46: 545-548.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* 46: 355-393.
- Morse, A.N.C. 1991. How do planktonic larvae know where to settle? *American Scientist* 79: 154-167.
- Morse, D.E. 1990. Recent progress in larval settlement and metamorphosis: closing the gaps between molecular biology and ecology. *Bulletin of Marine science* 46: 465-483.
- Morse, A.N.C. and Morse, D.E. 1988. Chemical signals and molecular mechanisms: learning from larvae. *Oceanus* 31:37-43.
- Morse, A.N.C. and Morse, D.E. 1984. Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surfaces of crustose red algae. *Journal of Experimental Marine Biology and Ecology* 75: 191-215.
- Nicotri, M.E. 1977. Grazing effect of four marine intertidal herbivores on the microflora. *Ecology* 58: 1020-1032.
- Padilla, D.K. 1985. Structural resistance of algae to herbivores. *Marine Biology* 90: 103-109.



- Round, F.E., Crawford, R.M. and Mann, D.G. 1990. The Diatoms. Biology & Morphology of Genera. Cambridge University Press, New York.
- Shepherd, S.A. and Daume, S. 1996. Ecology and survival of juvenile abalone in a crustose coralline habitat in South Australia. Pp. 297–313. In: Watanabe, Y., Yamashita, Y. and Oozeki, Y. Survival Strategies in Early Life Stages of Marine Resources. Balkema, Rotterdam.
- Southward, A.J. 1964. Limpet grazing and the control of vegetation on rocky shores. Pp. 265–273. In: Crisp, D.J. Grazing in terrestrial and marine environments. Blackwell Press, Oxford, England.
- Suzuki, H., Ioriya, T., Seki, T. and Aruga, Y. 1987. Changes of algal community on the plastic plates used for rearing the abalone *Haliotis discus hannai*. Nippon Suisan Gakkaishi 53(12): 2163–2167.
- Takami, H., Kawamura, T. and Yamashita, Y. 1997. Contribution of diatoms as food sources for post-larval abalone *Haliotis discus hannai* on a crustose coralline alga. Molluscan Research (This Issue).
- Takami, H., Kawamura, T. and Yamashita, Y. (1997b). Survival and growth-rates of post-larval abalone *Haliotis discus hannai* fed on conspecific trail mucus and/or benthic diatom *Cocconeis scutellum* var. *parva*. Aquaculture.
- Underwood, A.J. and Jernakoff, P. 1981. Effects of interaction between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia 48: 221–233.
- Underwood, A.J. 1984. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. Oecologia 64: 211–222.
- Woelkerling, W.J., Irvine, L.M. and Harvey, A.S. 1993. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). Australian Systematic Botany 6: 277–93.